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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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A CYTO-TAXONOMIC STUDY OF THE NORTH AMERICAN SPECIES OF MELICA

W. S. BOYLE

Recent students of experimental taxonomy have made it evident that a clear understanding of the taxonomy of any group of plants will be greatly facilitated by a knowledge of the cytology and breeding behavior of the species in question. The present study is an attempt to apply such data with the invaluable evidence gained from a study of morphology and geographic distribution, in order to define the specific lines and probable relationships of the North American species of *Melica*.

This group has had no revision since Scribner's brief synopsis in 1885 (9). A considerable mass of specimens which have never been studied as a unit has accumulated in the various herbaria of the country. The absence of polyploidy in the species of *Melica* studied by Stebbins and Love (11) made it desirable to investigate the cytology of as many species as possible in view of the fact that every other large, widespread, perennial genus in the Festuceae has polyploid species.

The problem has been approached from the following points of view. (1) The problem was first posed in relief by the usual herbarium study. (2) Karyotypes of fourteen of the seventeen species were obtained. In most species both haploid and diploid chromosome complements were studied and recorded. (3) The breeding behavior of the *Melica imperfecta*-*M. Torreyana*-*M. californica* complex was studied. (4) Thirteen of the seventeen species were observed in culture. (5) Eight of the western species were studied extensively in the field. No living material of *Melica Smithii*, *M. montezumae* or *M. spectabilis* has been seen.

It is a pleasure to acknowledge the substantial help which has been received during the course of this study. Dr. Herbert L. Mason has very generously given most valuable advice and direction. Dr. Lincoln Constance has extended very considerable help and encouragement throughout the study. In connection with the cytogenetic section and certain phases of the systematic treatment I am particularly indebted to Dr. G. Ledyard Stebbins, Jr.

Sincere thanks are also due to the curators of the following institutions (designated in the text by indicated initials) who have permitted me the loan of specimens under their care: Provincial Museum of Natural History, Victoria (BC); California Academy of Sciences (CA); Gray Herbarium, Harvard University (G); Missouri Botanical Garden (M); New York Botanical Garden (NY); University of Oregon (O); Dudley Herbarium, Stanford University (S); University of California (UC); United States National Herbarium (US); Vegetation Type Map Herbarium,

California Forest and Range Experiment Station, United States Forest Service, University of California (VTM); Rocky Mountain Herbarium, University of Wyoming (W); State College of Washington (WS).

CYTOGENETIC INVESTIGATIONS

Cytology

Diploid karyotypes were studied largely from root-tip sections and haploid from the first division of the pollen grain nucleus. Smears of root tips and intercalary meristems were utilized to a minor extent but these were much less satisfactory for study than the cut sections. The division of the generative nucleus proved less suitable than the division to form the generative and tube nuclei.

Anthers were taken from plants in the field or from plants grown in the greenhouse. Root tips were taken from potted plants either grown from seed or transplanted from the field. Collection stations and a key to the illustrated karyotypes are indicated in Table 1.

TABLE 1. KEY TO ILLUSTRATIONS OF MELICA KARYOTYPES AND SOURCES OF MATERIAL

Figure number	Species	Source of material
1	<i>M. Geyeri</i>	Napa County, California, <i>W. S. Boyle 1075</i>
2	<i>M. imperfecta</i>	Santa Clara County, California, <i>W. S. Boyle 1066</i>
3	<i>M. fugax</i>	Nevada County, California, <i>W. S. Boyle 1105</i>
4	<i>M. frutescens</i>	San Diego County, California, <i>A. A. Beetle 3151</i>
5	<i>M. Harfordii</i>	San Benito County, California, <i>G. L. Stebbins 2763</i>
6	<i>M. bulbosa</i>	Elko County, Nevada, <i>K. H. Beach 1564</i>
7	<i>M. stricta</i>	Elko County, Nevada, <i>K. H. Beach 1512</i>
8	<i>M. Torrejana</i>	Santa Clara County, California, <i>W. S. Boyle 1068</i>
9	<i>M. nitens</i>	Bexar County, Texas, <i>W. A. Silveus</i>
10	<i>M. mutica</i>	Durham, North Carolina, <i>G. L. Church</i>
11	<i>M. Porteri</i>	El Paso County, Colorado, <i>W. A. Silveus</i>

Root tips were killed and fixed according to Randolph's (8) modification of Navashin's fixative. After embedding in paraffin the tips were sectioned at 10 microns and stained with gentian violet. Smear preparations were made according to the iron-aceto-carmin method (4).

Drawings were made with the aid of a camera lucida at a magnification of 5000 \times . They are reproduced at 2500 \times .

The principal data obtained from the cytological study may be summarized as follows:

1. The diploid number eighteen, and haploid number nine, is constant in all species investigated.

2. There is little variation in karyotype between species.



PLATE I. CHROMOSOMES OF MELICA. 1, *M. Geyeri*; 2, *M. imperfecta*; 3, *M. fugax*; 4, *M. frutescens*; 5, *M. Harfordii*; 6, *M. bulbosa*; 7, *M. stricta*; 8, *M. Torreyana*; 9, *M. nitens*; 10, *M. mutica*; 11, *M. Porteri*. Haploid karyotypes from first division of the pollen grain nucleus; diploid, from root tip sections. All drawings made with camera lucida at 5000 \times and reproduced at 2500 \times .

3. The marked uniformity and stability of the chromosome complement in *Melica* constitute important evidence for retaining *Melica* as a distinct and well-marked genus.

4. Chromosome morphology and number have been of relatively small value in aiding the differentiation of specific lines within the genus.

The absence of polyploidy in *Melica* is most remarkable in view of the fact that practically all other large, widely distributed perennial genera of the Festuceae have polyploid species. Artificially induced autotetraploids and allotetraploids have been studied by Joranson (7). *Melica* will offer an almost unequalled opportunity for studying the differentiation and evolution of species in the Gramineae unencumbered by the complex problems of polyploidy and gross chromosome alteration.

The earliest cytological study of this genus was made by Avdulov (1), who investigated four European species. The karyotypes illustrated by Avdulov are basically similar to those of the North American species thus far known. The cytology of the North American species was completely unknown until as recently as 1941 when Stebbins and Love (11) studied seven species in connection with a cytological survey of California forage grasses. Karyotypes of *Melica aristata*, *M. subulata* and *M. californica* were illustrated. Since study of these three species by the author disclosed no additional information, illustrations of their karyotypes are omitted in this study.

Breeding Experiments

Aspects of the breeding behavior of one species complex (*Melica californica*, *M. Torreyana*, *M. imperfecta*) within the genus have been studied as far as the F_2 generation. The latter two species are very closely related and at the beginning of this study were thought probably to represent one ecospecies.

Two principal methods were used in producing the hybrids. (1) Interspersing the two species freely with one another as they approached anthesis. Hybrids were relatively easily detected by an intermediate condition of the rudiment, spikelet size and floret number. (2) Emasculation of the panicle of one species and surrounding this plant with members of the other species with which the cross was desired. Hybrids between *M. Torreyana* and *M. californica* were difficult to obtain. A sufficient number for reliable data was not obtained.

Hybrids were self-pollinated by enclosing the panicle in a glassine sack or by allowing the plant to reach anthesis and fruiting state in the open. Spikelets were harvested when mature and examined for seed content. The breeding results are summarized in Table 2. Each of the species was allowed to reproduce in order to afford evidence regarding fertility within the species. Representative results are indicated in Table 3.

TABLE 2. SUMMARY OF BREEDING RESULTS BETWEEN SELECTED SPECIES OF MELICA, F₁ GENERATION

	Florets produced	Caryopses produced
<i>M. imperfecta</i> and <i>M. Torreyana</i>		
Total selfed <i>imperfecta</i> × <i>Torreyana</i>	954	13
Total open <i>imperfecta</i> × <i>Torreyana</i>	3660	9
Total selfed <i>Torreyana</i> × <i>imperfecta</i>	523	9
Total open <i>Torreyana</i> × <i>imperfecta</i>	617	2
Grand total number of florets produced	5754	..
Grand total number of caryopses produced	33
Sterility: 99.4%		
<i>M. imperfecta</i> and <i>M. californica</i>		
Total selfed <i>imperfecta</i> × <i>californica</i>	194	14
Total open <i>imperfecta</i> × <i>californica</i>	877	6
Total selfed <i>californica</i> × <i>imperfecta</i>	133	12
Total open <i>californica</i> × <i>imperfecta</i>	173	19
Grand total number of florets produced	1377	..
Grand total number of caryopses produced	51
Sterility: 96.2%		

TABLE 3. SUMMARY OF BREEDING RESULTS WITHIN SELECTED SPECIES OF MELICA, F₁ GENERATION

	Florets produced	Caryopses produced
<i>M. imperfecta</i>		
Total selfed	161	144
Total open	800	605
Grand total	961	749
Sterility: 22.0%		
<i>M. Torreyana</i>		
Total selfed	373	320
Total open	110	57
Grand total	483	377
Sterility: 21.8%		
<i>M. californica</i>		
Total selfed	452	178
Total open	43	21
Grand total	495	199
Sterility: 59.8%		

The F₁ hybrids were vigorous in all crosses; heterosis was usually exhibited. Pollen sterility of the hybrids ranged from 75 per cent to 86 per cent. Pollen sterility of the species ranged from 2 per cent to 9 per cent.

The more significant characteristics of these three species are summarized in the following points:

1. *Melica Torreyana* and *M. imperfecta* are able to cross. The hybrids are vigorous and almost completely sterile.

2. *Melica imperfecta* and *M. californica* are able to cross. The hybrids are likewise vigorous and almost completely sterile.

3. The F_2 generation exhibits a definite decrease in vigor.

4. The species are relatively highly fertile: *M. Torreyana*, 78 per cent; *M. imperfecta*, 75 per cent; *M. californica*, 40 per cent.

5. Herbarium and field studies indicate marked morphological discontinuity between *M. imperfecta*, *M. Torreyana*, *M. californica*.

6. A moderate but not marked amount of geographic and ecologic segregation exists between these species.

Each of these three entities is worthy of specific rank. They have morphological discontinuity; their hybrids are nearly sterile and have weakened vigor in the F_2 generation; they exhibit a moderate amount of geographic and ecologic segregation.

RELATIONSHIPS AND PHYLOGENY

The natural relationships of *Melica* present a perplexing problem. Morphologically, the monotypic genus *Schizachne* most closely approaches *Melica*. It has in fact been united with *Melica* by some authors. Investigation of the cytology of *Schizachne* by the author (2) afforded evidence for its exclusion from *Melica*.

Skorniakov and co-workers (10) have suggested that *Melica*, *Schizachne*, *Pleuropogon*, *Glyceria* and *Anthocloa* constitute a natural group and should be segregated as the tribe Melicineae. As thus constituted the Melicineae, in their opinion, serve as a connecting link between the Aveneae and Bromeae. In addition, they are of the opinion that the true relationships of *Melica* are with the Aveneae and not the Festuceae.

This viewpoint has much to recommend it. The common possession by the above genera of united, collar-like lodicules, dichotomously branching stigmas, glabrous caryopses, weak glumes and firm lemmas strongly suggests closer genetic relationship than students of the Gramineae have thus far ascribed to these genera.

The most primitive features of the genus are exhibited by *M. Smithii*, *M. subulata* and *M. Harfordii*. They have large spikelets with several florets, lemmas awned or long attenuate and sterile florets similar to the fertile. The most highly specialized features are exhibited by *M. mutica*, *M. montezumae*, *M. imperfecta* and *M. Torreyana*. Their characteristics include convolute and club-shaped sterile florets, development of articulation below the glumes (in the former two species), and reduction in size and number of florets. The section Eumelica as herein defined, is regarded as a specialized offshoot from the other more primitive North American species.

While a discussion of the relationships of the South American, European and Asiatic species of *Melica* is outside the scope of this study, certain general relationships can be indicated. These

species all seem clearly to belong to specialized groups judging from their similarity to the North American *M. mutica*, *M. nitens* and *M. montezumae*. With the exception of *M. subulata* (which is probably an introduction) all of the South American species apparently belong to the section *Eumelica*.

Although investigations upon the geologic history of this group are incomplete, the author is inclined to believe that *Melica* had its origin in northwestern America and that there was a subsequent migration eastward and southward.

TAXONOMIC TREATMENT

The earliest taxonomic study involving North American species of *Melica* was contained in a short discussion of the Californian species by Bolander (3) in 1870. The North American species were first treated as a unit by Scribner (9) in 1885. Scribner divided the genus into three sections based on floret number, texture and nervation of the lemma and presence or absence of awns. This division of the genus is here considered unsound since these criteria do not provide a basis for a natural division of the genus. Scribner's concept of species within the genus, however, is largely satisfactory.

Farwell (5) proposed the genus *Bromelica* to include certain species of *Melica* and *Schizachne purpurascens*. Species in *Bromelica* were then presumably characterized by non club-shaped rudiments, membranous glumes and lemmas, and awned or notched lemmas. These criteria were found not to be distinctive when compared with the remaining *Melica* species. Cytological evidence previously discussed indicates that *Schizachne* should be segregated from *Melica* and that *Melica* as defined in the present study constitutes a natural unit.

Hitchcock (6, 193-204) followed Scribner's treatment closely in delimiting specific lines. The significant changes are rearrangement of the subgenera and keys, a more detailed review of the synonymy and additional information on the distribution of the species. Two of Scribner's subgenera are retained by Hitchcock but their descriptions were emended as follows: *Bromelica* with narrow spikelets, acute or awned lemmas (except *Melica Harfordii*); *Eumelica* with broad spikelets and obtuse or awnless lemmas. This division of the genus is likewise considered faulty. The character of narrow spikelets applies to *Melica Porteri*, *M. Torreyana*, *M. fugax*, *M. californica*, *M. frutescens* and *M. bulbosa*, all of which were placed in *Eumelica* by Hitchcock. Acute lemmas are not uncommon in *M. Torreyana*, *M. spectabilis* and *M. bulbosa*, yet these species were placed in *Eumelica*.

It is evident that a new arrangement of the species in the sections is necessary. The genus may be divided naturally and easily on the basis of striking differences in the articulation of the spikelets. In five species the articulation is almost invariably

below the glumes, allowing the spikelet to fall as a whole at maturity. In the remainder of the species the articulation is almost invariably above the glumes. It is here proposed, therefore, that the species in which the articulation is below the glumes be segregated as the Section *Eumelica* and those in which the articulation is above the glumes as the Section *Bromelica*.

MELICA L. Fl. Lappon. 23. 1737. *Chondrachyum* Nees, Lindl. Introd. Nat. Cyst. 11: 449. 1836. *Dalucum* Adans. Fam. ii: 323. 1763. *Bromelica* Farwell, Rhodora 21: 77. 1919.

Perennial; culms frequently bulbous at the bases, often attached to a rhizome; sheaths closed, blades flat; ligule 1 to 10 mm. long, often lacerate and decurrent; panicle simple or compound, very narrow to widely spreading; spikelets 1- to 6-flowered, articulation above or below the glumes; terminal floret or florets sterile, similar to fertile florets or reduced to an obovoid, blunt rudiment; glumes less firm than the lemmas, margins and apices hyaline or papery, not keeled, obtuse to acute, 3- to 5-nerved, in some species equaling the spikelet; lemmas firm, not keeled, the apices and upper margins hyaline, usually 7-nerved, awned or awnless; awn if present straight, occasionally from a bifid apex; palea usually three-fourths the length of lemma, rarely as short as one-half as long; callus glabrous; lodicule a truncate, collar-like scale; stigmas dichotomously branched; caryopsis smooth and shining, free.

KEY TO THE NORTH AMERICAN SPECIES OF MELICA

- | | |
|--|-----------------------------|
| Articulation above the glumes and between the florets . . . | Section 1. <i>Bromelica</i> |
| Articulation below the glumes, spikelet at maturity falling entire | Section 2. <i>Eumelica</i> |

SECTION 1. BROMELICA

- | | |
|--|------------------------|
| A. Lemmas awned. | |
| B. Awn short, usually less than 4 mm. long; blades long and narrow; lemma narrowing to an obtuse and often emarginate apex; lower margin of lemma usually densely ciliate-pubescent . . . | 3. <i>M. Harfordii</i> |
| BB. Awn longer, usually 5-9 mm. long, blades short, or if long at least 6 mm. wide; apex of lemma not obtuse; lower margin of lemma glabrous, scabrous or only slightly ciliate. | |
| C. Panicle narrow, the branches appressed to ascending; blades short, usually about 9 cm. long, very rarely more than 5 mm. wide; brownish swelling in axils of panicle branches none | 4. <i>M. aristata</i> |
| CC. Panicle broad; branches widely spreading to often reflexed; blades long, usually about 18 cm. long and from 6 to 15 mm. wide; a small brownish swelling present in axils of panicle branches | 5. <i>M. Smithii</i> |
| AA. Lemmas not awned. | |
| D. Culms bulbous at the bases. | |

- E. Lemmas tapering-acuminate, usually strongly so, almost invariably ciliate-pubescent on the nerves 1. *M. subulata*
- EE. Lemmas merely acute or obtuse, glabrous.
 F. Rachilla swollen, usually wrinkled in drying 6. *M. fugax*
- FF. Rachilla normal, not swollen.
 G. Panicle at maturity open and broad, branches long and spreading; first and second florets about 2.5 mm. apart; spikelets usually about 16 mm. long 2. *M. Geyeri*
- GG. Panicle narrow or only slightly spreading; first and second florets rarely as much as 2 mm. apart; spikelets usually considerably less than 16 mm. long.
 H. Bulb of the culm small, globose, "tailed" at base, i.e., bulb not attached directly to rhizome; first glume less than half as long as the spikelet 7. *M. spectabilis*
- HH. Bulb of the culm attached directly to rhizome (if rhizome present); first glume more than half as long as spikelet.
 I. Panicle very narrow, the branches and spikelets appressed.
 J. Rudiment almost always blunt; not exserted; culms more or less swollen towards the base and usually constricted in one or more places; no woody rhizome present; coast ranges and foothills of the Sierra Nevada of California 8. *M. californica*
- JJ. Rudiment tapering above, almost invariably slightly exserted; culms more or less bulbous at the bases and attached directly to a woody rhizome, the latter usually present in older plants; higher elevations (usually above 4000 feet), Pacific Coast and as far

- east as the Rocky Mountains 9. *M. bulbosa*
- II. Panicle somewhat spreading, the branches stiffly ascending; spikelets pale; lemmas strongly nerved 9a. *M. bulbosa* var. *inflata*
- DD. Culms not bulbous at the bases.
- K. Fertile florets 1 or 2.
- L. Rudiment 1 mm. long, on a stipe 2.5 mm. long, this usually slightly swollen; lemma pubescent near the tip . . . 10. *M. Torreyana*
- LL. Rudiment usually 2 mm. or more in length, on a short unswollen stipe 0.5 mm. long, lemma glabrous or scabrous 11. *M. imperfecta*
- KK. Fertile florets more than 2.
- M. Lemmas pilose-ciliate on the lower margins 3. *M. Harfordii*
- MM. Lemmas glabrous or scabrous.
- N. Palea about half the length of the lemma; spikelets often pale and shining, usually about 14 mm. long; plant tall, robust, desert regions 12. *M. frutescens*
- NN. Palea three-fourths the length of the lemma; spikelets usually about 1 cm. long.
- O. Rudiment almost always blunt, not exerted; culms more or less swollen towards the base and usually constricted in one or more places; no woody rhizome present; coast ranges and foothills of the Sierra Nevada of California 8. *M. californica*
- OO. Rudiment tapering above, almost invariably slightly exerted; culms attached directly to a woody rhizome, the latter usually present in older plants; higher elevations (usually above 4000 feet), Pacific Coast and as far east as the Rocky Mountains . . . 9. *M. bulbosa*

SECTION 2. EUMELICA

- A. Rudiment blunt, club-shaped or obconic, very rarely tapering above.
- B. Spikelets with 1 perfect floret; back of lemma bearing a group of flat, twisted hairs 13. *M. montezumae*
- BB. Spikelets with more than 1 perfect floret; lemmas glabrous or scabrous.
- C. Panicle simple, rarely compound; rudiment almost invariably bent at an angle

- to the rachilla; interior sterile lemmas extruding; apices of fertile florets very nearly the same height 14. *M. mutica*
- CC. Panicle usually compound; branches spreading; rudiment never bent at an angle toward rachilla; interior sterile lemmas very rarely extruding; apices of fertile florets not the same height 15. *M. nitens*
- AA. Rudiment almost invariably tapering above, not blunt, club-shaped or obconic.
- D. Spikelets broadly V-shaped when mature, glumes as long or nearly as long as the spikelet 16. *M. stricta*
- DD. Spikelets narrow, florets appressed; glumes one-half to two-thirds the length of the spikelet 17. *M. Porteri*

1. *MELICA SUBULATA* (Griseb.) Scribn. Proc. Acad. Nat. Sci. Phila. 37: 47. 1885. *Bromus subulatus* Griseb. Ledeb. Fl. Ross. 4: 358. 1853. *Melica acuminata* Boland. Proc. Calif. Acad. Sci. 4: 104. 1870. *M. Pammelii* Scribn. Proc. Davenport Acad. Sci. 7: 240. 1899. *Bromelica subulata* Farwell, Rhodora 21: 78. 1919.

Culms up to 125 cm. long, bulbous at the bases and attached to a rhizome; blades 2–10 mm. wide, panicle 8–25 cm. long, averaging 16 cm., usually narrow, occasionally spreading, branches rarely longer than 9 cm.; spikelets 10–28 mm. long, averaging 18 mm., florets 2–5, loosely flowered; glumes acute to sub-acute, first glume 4–7 mm. long, averaging 5 mm., second glume 6–9 mm. long, averaging 7.5 mm., very thin, purple- or brown-tinged; lemmas narrowed above to a long attenuate apex, rarely merely acute, not awned, almost invariably pilose-ciliate on the backs, first lemma 8–15 mm. long, averaging 11 mm.; anthers 2 mm. long; caryopses 4–5 mm. long; rudiment long, tapering above 4–9 mm. long, averaging 6 mm.

Type. Unalaska, *Eschscholtz* 4. The type has not been seen.

Range. Central California northward to Alaska, southeastward in the Rocky Mountains to Sheridan County, Wyoming; also recorded from Chile; distributed chiefly in moist woods, on banks, and on shady slopes.

Representative specimens. CALIFORNIA. Butte County: Jonesville, *Copeland* 338 (UC, G, M, NY, OW, S). Humboldt County: Humboldt Bay, *Chandler* 1174 (UC, G, M, NY, S). Sonoma County: near Occidental, *Boyle* 1097. OREGON. Blue Mountains, *Cusick* 3249 (UC, NY, WS, O, US, W, S). WASHINGTON. Clallam County: Olympic Mountains, *Elmer* 1937 (UC, WS, O, BC, M, NY, S); Island County: Cranberry Lake, *Hitchcock* 3468 (UC, NY, WS, W, CA, S).

Melica subulata is related most closely to *M. Geyeri*. Detailed field studies have indicated no evidence of natural crossing.

2. *MELICA GEYERI* Munro ex Boland. Proc. Calif. Acad. Sci. 4: 103. 1870. *M. bromoides* var. *Howellii* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 47. 1885. *Bromelica Geyeri* Farwell, Rhodora 21: 78. 1919. *B. Geyeri* var. *Howellii* Farwell, Rhodora 21: 78. 1919.

Culms up to 200 cm. tall, bulbous at bases and attached to rhizomes; blades 2–8 mm. wide, often short pubescent on upper surfaces; panicle 11–27 cm. long, averaging 18 cm., at maturity loose, spreading, branches distant, spreading to reflexed, up to 14 cm. long; spikelets 8–24 mm. long, averaging 17 mm., florets 2 to 6, loosely flowered; pedicels often flexuous; glumes sub-acute, first glume 3.5–7 mm. long, averaging 5 mm., second glume 5.5–11 mm. long, averaging 7 mm., bronze or purple-tinged; lemmas usually sub-acute, first lemma 8–11 mm. long, averaging 9 mm., often bronze or purple-tinged; anthers 3–4 mm. long; caryopses 4 mm. long; rudiment narrow, tapering above, 3–7 mm. long, averaging 5 mm.

Type. "Russian River Valley [Ukiah, Mendocino County], California," Bolander. "No. 40 of my small collection and no. 6119 of the Catalogue, 1867" (UC).

Range. Principally in the coast ranges from Monterey County, California, to northern Oregon; rare in the central Sierra Nevada; chiefly in dry open woods.

Representative specimens. CALIFORNIA. Glenn County: Benet Spring, Heller 11932 (G, M, NY, CA, S). Mendocino County: Ukiah, Bolander 40 (UC, type; G, NY, M). Napa County: Calistoga, Boyle 1072. OREGON. Josephine County: near Selma, Henderson 5761 (M, O, W, CA, S).

3. *MELICA HARFORDII* Boland. Proc. Calif. Acad. Sci. 4: 102. 1870. *M. Harfordii* var. *minor* Vasey, Bull. Torrey Bot. Club 15: 48. 1888. *M. Harfordii* var. *tenuior* Piper, Contr. U. S. Nat. Herb. 11: 127. 1906. *Bromelica Harfordii* Farwell, Rhodora 21: 78. 1919. *B. Harfordii* var. *minor* Farwell, Rhodora 21: 78. 1919. *Melica Harfordii* var. *tenuis* Suksdorf, Werdenda 1: 17. 1927. *M. Harfordii* var. *viridifolia* Suksdorf, Werdenda 1: 17. 1927.

Culms up to 120 cm. long, densely tufted, blades 2–6 mm. wide, extending widely from culms, as long as 30 cm., averaging 16 cm.; panicle 6–23 cm. long, averaging 15 cm., narrow; spikelets 7–20 mm., averaging 13 mm.; florets 2 to 6; glumes obtuse to sub-acute, first glume 4–10 mm. long, averaging 7 mm., second glume 5–11 mm. long, averaging 8.5 mm., lemmas usually short-awned, awns fragile and usually less than 5 mm. long, pilose ciliate on lower margin, first lemma 6–16 mm. long, averaging 9 mm., apices emarginate, obtuse or narrowly rounded; anthers 3–4 mm. long; caryopses 5 mm. long; rudiment narrow, tapering above, 3–5 mm. long.

Type. "Santa Cruz Mountains near State Road, eastern side



FIG. 1. Distribution of *Melica* in North America.

in Redwoods [near Lexington], California," June, 1865, *Bolander* 53 (CA).

Range. Principally in the coast ranges from British Columbia south to Monterey County, occasionally in the central Sierra Nevada below 7000 feet; distributed chiefly on dry slopes or in dry open woods.

Representative specimens. CALIFORNIA. Marin County: Mt. Tamalpais, *Long* 189a (UC, NY, WS, W, CA). Mendocino County: Panther Springs, *Boyle* 1081. OREGON. Ashland Butte, *Cusick* 2887 (UC, NY, WS, O, M). Curry County: Port Orford, *Peck* 8643 (G, M, NY, O). WASHINGTON. Clallam County: Olympic Mountains, *Elmer* 1938 (UC, NY, WS, O, M, BC, S).

Melica Harfordii var. *minor* is here considered simply as applicable to depauperate members of the species. *Melica Harfordii* var. *tenuis* Suksdorf has no valid basis, morphological or geographical. *Melica Harfordii* var. *tenuior* Piper is based on var. *minor* Vasey.

4. *MELICA ARISTATA* Thurb. ex Boland. Proc. Calif. Acad. Sci. 4: 103. 1870. *Bromelica aristata* Farwell, Rhodora 21: 77. 1919.

Culms up to 120 cm. long, densely tufted; sheaths pilose to glabrous; blades short, 6–14 cm. long, averaging 9 cm., 3–6 mm. usually narrow; panicle 10–23 cm. long, averaging 15 cm., spikelets 11–20 mm. long, averaging 14 mm., florets 2 to 3; glumes obtuse to sub-acute, first glume 7–11 mm. long, averaging 9 mm., second glume 7–12 mm. long, averaging 10 mm.; lemmas awned, awns 5–12 mm. long, averaging 9 mm., first lemma 8–13 mm. long, averaging 11 mm., glabrous to slightly ciliate pubescent on lower margins; anthers 2–3 mm. long; caryopses 5–6 mm.; rudiment narrow, tapering above, usually awned, 2.5–6 mm. long.

Type. "Open woods at Clark's" [Wawona], California, June 6 to September, 1866, *Bolander 4861* (UC).

Range. Principally in the Sierra Nevada and Cascade ranges from southern Washington to Tulare County, California; chiefly in dry open woods.

Representative specimens. CALIFORNIA. Butte County: Jonesville, *Copeland 337* (UC, G, M, NY, W, O, US, CA, S). Mariposa County: Clark's, *Bolander 4861* (UC, type; M). Tulare County: Bearpaw Meadow, *Long 229a* (UC, NY, W, WS, BC, CA). OREGON. Jackson County: Farewell Bend, *Hitchcock 4963* (NY, WS, S).

Melica aristata is most closely related to *M. Smithii* and *M. Harfordii*. The very short blades are distinctive.

5. *MELICA SMITHII* (Porter) Vasey, Bull. Torrey Bot. Club 15: 294. 1888. *Avena Smithii* Porter, A. Gray, Man. ed. 5: 640. 1867. *Melica retrofracta* Suksdorf, Deut. Bot. Monatschr. 19: 92. 1901. *Bromelica Smithii* Farwell, Rhodora 21: 77. 1919.

Culms up to 150 cm. long, loosely tufted, attached to rhizomes, blades lax, 6–15 mm. wide; panicle 13–40 cm. long, averaging 23 cm., open, branches widely spreading to often reflexed, branches rarely in pairs, small brownish swelling in axil of each branch; spikelets 12–20 mm. long, averaging 14 mm., florets 2 to 6, usually 3; glumes acute, first glume 3–6 mm. long, averaging 5 mm., often entirely brown-tinged, second glume 5–9 mm. long, averaging 7 mm.; lemmas awned from bifid apices, awns up to 10 mm. long, averaging 5 mm.; first lemma 9–14 mm. long, averaging 10 mm.; rudiment long, narrow, tapering above, 3.5–6 mm. long, averaging 5 mm.

Type. Woods, Sault Ste. Marie, Michigan, *C. E. Smith*. A photograph of the type which is located in the Academy of Natural Sciences at Philadelphia has been seen.

Range. Southern British Columbia and Alberta, Washington, Oregon, Idaho, Montana and the northern Great Lakes region; specimens have been reported from the Black Hills, South Dakota; cool, moist woods.

Representative specimens. MICHIGAN. Beech-maple forest, *Gleason 18* (G, NY). WYOMING. Teton Mts., *Nelson 6524* (G, NY, M). OREGON. Baker County: Paddys Creek, *Cusick 2239* (UC, G, M, O, WS, US). WASHINGTON. Skamania County: shady places, *Suksdorf 2334* (UC, G, M, O, WS).

6. *MELICA FUGAX* Boland. Proc. Calif. Acad. Sci. 4: 104. 1870. *M. fugax madophylla* Piper, Contr. U. S. Nat. Herb. 11: 128. 1906. *M. Macbridei* Rowland, Bot. Gaz. 54: 404. 1912. *M. fugax* var. *inexpansa* Suksdorf, Werdenda 1: 1. 1923.

Culms short, occasionally to 65 cm. long, prominently bulbous at bases, usually aggregated together and attached to a light rhizome; blades 2-4 mm. wide; panicle 8-18 cm. long, averaging 10 cm., the short branches widely spreading or appressed; spikelets 4-17 mm. long, averaging 8 mm., florets 2 to 4, loosely flowered, rachilla remarkably swollen, spongy and usually wrinkled in drying; glumes obtuse, first glume 3-5 mm. long, averaging 3.5 mm., second glume 3.5-7 mm. long, averaging 5 mm.; first lemma 4-7 mm. long, averaging 5 mm.; anthers 1-2 mm. long; rudiment narrow, tapering above, 2-3.5 mm. long.

Type. Donner Lake, June, 1869, *Bolander* (G).

Range. Central California to central Oregon east to western Idaho; dry open flats and hillsides or open dry woods, usually on soil of volcanic origin, rarely below 4000 feet.

Representative specimens. CALIFORNIA. Donner Lake, 1869, *Bolander* (G, type; M, NY). Placer County: Yuba River, Cisco, *Heller 12699* (G, M, NY, S). Nevada County: Hobart Mills, *Boyle 1105*. OREGON. Crook County: Summit Prairie, *Cusick 2644* (UC, G, M, NY, O, W, S). IDAHO. Owyhee County: Silver City, *Macbride 948* (UC, G, M, BC, W, S).

The narrow paniced form, while actually common and widespread, has received very little attention in the literature. Suksdorf described the variety *inexpansa* on this character. Specimens possessing this feature have no distinct geographic segregation and intermediate forms are common. It is not here recognized as varietally distinct.

Melica fugax var. *madophylla* Piper is presumably distinguished by the glabrous culms and foliage. Pubescence varies widely in *M. fugax* and there is no geographic segregation of plants possessing this character.

7. *MELICA SPECTABILIS* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 45. 1885. *M. scabrata* Scribn. in Piper, Fl. Palouse 25. 1901.

Culms up to 100 cm. long, bulbous at bases, the bulbs not attached directly to rhizome but each bulb connected to it by a slender stem; blades 2-5 mm. wide; panicle 5-26 cm. long, averaging 14 cm., narrow to occasionally open, branches often somewhat flexuous; spikelets 7-19 mm. long, averaging 11 mm., florets

3 to 7, turgid; pedicels capillary and often flexuous; glumes obtuse to sub-acute, first glume 3.5–5.5 mm. long, averaging 5 mm., and less than one-half as long as the spikelet, second glume 5–7 mm. long, averaging 6 mm.; lemmas sub-acute or obtuse, first lemma 6–9 mm. long, averaging 7 mm., very broad, lemmas distinctly purple-tinged below the brownish scarious apex, nerves prominent; anthers 2 mm. long; caryopses 3 mm. long; rudiment 1.5–3.5 mm. long, apex narrowed to a small scarious beak, rarely exerted.

Type. Crow Mountains, Montana, 6000 feet, *F. L. Scribner 385*, 1883. The type is presumably in the United States National Herbarium.

Range. Northern California in the coast ranges eastward to Laramie County, Wyoming, south to the La Salle Mountains in southern Utah and northward to British Columbia; chiefly in moist meadows or open woods, rarely below 4000 feet.

Representative specimens. COLORADO. Mt. Richthofen, Colo. State College Herb. 3602 (UC, G, NY, US, WS, W, BC). IDAHO. Fremont County: Ponds Lodge, *Hitchcock 3855* (UC, WS, W, S). MONTANA. Bridger Mts., *Rydberg* and *Bessey 3610* (G, NY, W, BC). OREGON. Wallowa Mts., *Cusick 3180* (UC, G, M, NY, WS, O, W). WYOMING. Albany County: Medicine Bow Mts., *Nelson 7747* (G, M, NY, O, W, CA).

Melica spectabilis is most closely related to *M. bulbosa* and is commonly confused with it. The marked contrast of the attachment of the bulb to the rhizome and the comparative length of the glumes and lemmas afford immediate key characters for separation.

8. *MELICA CALIFORNICA* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 46. 1885. *M. poaeoides* Nutt. (misapplied by Torrey) U. S. Rep. Expl. Miss. Pac. 4: 157. 1857. Not *M. poaeoides* Nutt. Jour. Acad. Nat. Sci. Phila. ser. 2, 1: 188. 1848 = *M. imperfecta* Trin. *M. bulbosa* Geyer; Thurb. in S. Wats. Bot. Calif. 2: 304. 1880. Not *M. bulbosa* Geyer; Porter and Coulter, Syn. Flora Colo. 149: 1874 which equals no. 9 of this revision. *M. longiligula* Scribn. and Kearn. U.S.D.A. Bull. Div. Agrost. 17: 225. 1899.

Culms up to 130 cm. long, not definitely bulbous at bases but almost invariably enlarged in the lower portions, usually constricted in one or more places near the bases, densely tufted; blades 2–5 mm. wide; ligule 2–5 mm. long; panicle 4–30 cm. long, averaging 18 cm., very narrow, usually dense, often interrupted below; spikelets 5–15 mm. long, averaging 10 mm., florets 2 to 5, usually 3, chaffy, appearing papery; glumes subequal, first glume 3.5–12 mm. long, averaging 6 mm., second glume 5–13 mm. long, averaging 7.5 mm., occasionally equalling or even exceeding spikelet; lemmas obtuse, emarginate or rarely acute, first lemma 5–9 mm. long, averaging 7.5 mm.; anthers 3 mm. long; caryopses

3 mm. long; rudiment usually blunt or obovoid, rarely tapering above, not exserted, 1–3 mm. long.

Type. Santa Ynez, California, *W. H. Brewer 569* (G).

Range. Coast ranges and lower Sierra Nevada of California; distributed chiefly on dry, rocky, exposed hillsides.

Representative specimens. CALIFORNIA. Mendocino County: South Fork Eel River, *Boyle 1084*. Santa Barbara County: Santa Ynez, *Brewer 569* (G, type). Santa Clara County: Mt. Hamilton, *Elmer 4304* (UC, M, NY, WS, O, CA, S). Sonoma County: *Heller 5351* (M, NY, S). Stanislaus County: Arroyo del Puerto, *Sharrsmith 1764* (UC, WS).

The complex synonymy of *Melica californica* was largely clarified by Hitchcock (6, p. 882).

Melica californica may be considered an ecospecies possessing at least two ecotypes and possibly a third. One ecotype occupies the coast ranges of northern, central and south central California; another occupies the foothills of the Sierra Nevada and is here designated as the new variety *nevadensis*. The third entity occupies the southern California coast ranges and is possibly of ecotype status. There is not sufficient geographic segregation as seen from herbarium specimens, to warrant its designation as an ecotype.

8a. *MELICA CALIFORNICA* var. *nevadensis* var. nov. Spiculae nonnihil sicut V-formatae; glumae acutae, floritumque ultimum saepe excedens; panícula densissima, spiculae specie breviores.

This variety differs from the species in the following characters: (1) spikelet tends to be slightly V-shaped; (2) glumes acute and often exceeding last floret; (3) panicle very dense, especially above; (4) rudiment very blunt, usually truncate; (5) spikelets shorter (average 8 mm.) than in the species.

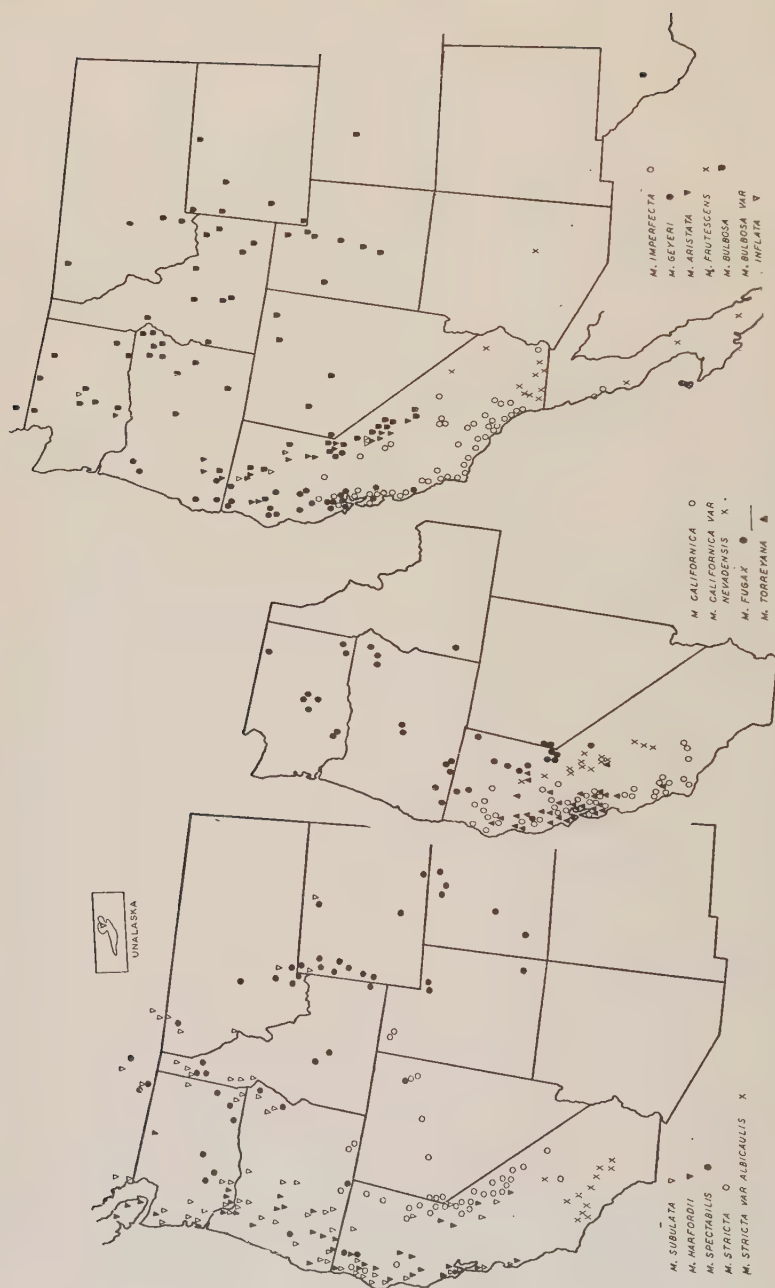
Type. One-half mile northwest of Central Ferry, Calaveras County, California, April 25, 1935, *J. A. Rutter 163* (VTM).

Range. In the lower Sierra Nevada of California, almost entirely below 4000 feet.

Representative specimens. CALIFORNIA. Amador County: near Jackson, *Hansen 631* (UC, M, S). Butte County: Butte Creek, *Heller 11860* (UC, M, NY, CA, S). Calaveras County: Central Ferry, *Rutter 163* (VTM, type). Tuolumne County: *Keck and Clausen 5269* (G, S).

9. *MELICA BULBOSA* Geyer, Porter and Coulter, Syn. Fl. Colo. 149. 1874. *M. bulbosa* Geyer, ex Hook. Jour. Bot. Kew Misc. 8: 19. 1856. *M. bulbosa* Gray, Proc. Am. Acad. Sci. 8: 409. 1872. *M. bella* Piper, U.S.D.A. Div. Agr. Circ. 27: 10. 1900. *M. bella intonsa* Piper, Contr. U. S. Nat. Herb. 11: 128. 1906. *M. bulbosa* var. *caespitosa* Cronquist, Madroño 7: 77. 1943.

Culms up to 60 cm. tall, usually bulbous at the bases, bulbs attached directly to a woody rhizome, the latter usually present

FIG. 2. Distribution of *Melica* in North America.

in older plants; blade 2–5 mm. wide; panicle usually very narrow, rarely bearing more than twenty-five spikelets; spikelets 6–24 mm. long, averaging 11 mm.; florets 2 to 5, usually 3; glumes obtuse to acute, first glume 5–9 mm. long, averaging 7 mm., second glume 6–10 mm. long, averaging 7.5 mm., glumes two-thirds to three-fourths as long as spikelet, never as long; lemmas usually obtuse, first lemma 6–11 mm. long, averaging 8 mm., distinctly purple-tinged below the scarious apex; anthers 4 mm. long; rudiment narrow, tapering above, exserted, 1.5–5 mm. long, averaging 3 mm.

Type. "Rocky ravine, upper Platte," *Geyer 11* (G).

Range. South central Sierra Nevada in California northward to British Columbia and eastward to Colorado and Jeff Davis County, Texas; chiefly on dry, rocky slopes and in open dry woods; extends to alpine regions.

Representative specimens. CALIFORNIA. Humboldt County: Trinity Summit, *Tracy 14194* (UC, G, S). Tulare County: Aster Lake, *Long 239a* (UC, NY, CA). OREGON. Crook County: Grizzly Butte, *Leiberg 268* (G, W, NY, S). WASHINGTON. Kittitas County: west of Ellensburg, *Hitchcock* and *Martin 3414* (UC, WS, W, CA, S). WYOMING. Sublette County: Piney Mt., *Payson 2715* (UC, G, M, NY, W).

9a. *MELICA BULBOSA* var. *inflata* (Boland.) comb. nov. *M. poaeoides* var. *inflata* Boland., Proc. Calif. Acad. Sci. 4: 101. 1870. *M. inflata* (Boland.) Vasey, Contr. U. S. Nat. Herb. 1: 269. 1893.

This variety differs from the species in the wider panicle with longer, stiffly ascending branches, spikelets pale and larger (averaging 16 mm. long) and lemmas acute and strongly nerved.

Range. Central Sierra Nevada northward to central Washington; chiefly in meadows or shady woods, rare.

Type. Yosemite Valley, California, *Bolander 6121* (UC).

Representative specimens. CALIFORNIA. Yosemite Valley, *Bolander 6121* (UC, type; G); Yosemite, Hog Ranch, *Hall* and *Babcock 3334* (UC, NY). Tuolumne County: Mather, *Keck 1109* (G, M, CA, S). WASHINGTON. Chelan County: Blewett Pass, *Thompson 6296* (G, US).

This entity possibly represents a meadow ecotype of the more xeric *M. bulbosa*. Intergrading forms between this variety and the species are common.

10. *MELICA TORREYANA* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 43. 1885. *M. imperfecta* var. *sesquiflora* Torrey in herb.

Culms weak, slender, up to 100 cm. long, usually in dense clumps; blades lax, 1–4 mm. wide; panicle 8–25 cm. long, averaging 14 cm. long, branches appressed or occasionally spreading; spikelets 4–7 mm. long, averaging 5.5 mm., florets usually 1, occasionally 2; glumes nearly as long or occasionally longer than last

floret, usually acute, first glume 3.5–5 mm. long, averaging 4.5 mm., second glume 3.5–7 mm. long, averaging 5 mm.; lemmas sub-acute, pubescent on upper dorsal surfaces, first lemma 4–6 mm. long, averaging 4.5 mm.; palea usually as long as lemma; anthers 2–3 mm. long; caryopses 3 mm. long; rudiment small, blunt-oblong, 0.5–1.5 mm. long, stipe much longer than rudiment, 1.5–4 mm. long.

Type. San Francisco, California, *H. N. Bolander*, Kellogg and Co. 1872. The type is presumably in the U. S. National Herbarium.

Range. Chiefly in the coast ranges of California from San Luis Obispo County northward to Humboldt County, rare in the Sierra Nevada from Mariposa County, to Butte County; distributed principally in thickets, shady woods.

Representative specimens. CALIFORNIA. Alameda County: Berkeley hills, *Long 165a* (UC, NY, WS, W, BC, CA). Butte County: Centerville, Berry Canyon, *Heller 5511* (G, M, W, S). Marin County: Mt. Tamalpais, *Heller 8397* (G, M, NY, CA, S); Tiburon Peninsula, 1926, *Parks* (UC, NY, CA, S). Napa County: Petrified Forest, *Boyle 1076*. Santa Clara County: Los Gatos Canyon, *Heller 742* (UC, G, M, NY, W, S).

11. *MELICA IMPERFECTA* Trin. Mem. Acad. St. Petersburg. VI. Sci. Nat. 2¹: 59. 1836. *M. colpodoides* Nees, Ann. Nat. Hist. 1: 283. 1838. *M. panicoides* Nutt. Jour. Acad. Nat. Sci. Phila. Ser. 2, 1: 188. 1848. *M. poaeoides* Nutt. Jour. Acad. Nat. Sci. Phila. Ser. 2, 1: 188. 1848. *M. imperfecta* var. *flexuosa* Boland. Proc. Calif. Acad. Sci. 4: 101. 1870. *M. imperfecta* var. *refracta* Thurb. in S. Wats. Bot. Calif. 2: 303. 1880. *M. imperfecta* var. *minor* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 42. 1885. *M. Parishii* Vasey; Beal, Grasses N. Am. 2: 500. 1896. *M. imperfecta* var. *pubens* Scribn. U.S.D.A. Div. Agrost. Circ. 30: 8. 1901.

Culms up to 110 cm. tall, densely tufted; blades 1–6 mm. wide, average 3 mm.; ligule 3–6 mm. long, panicle 5–36 cm. long, averaging 19 cm., narrow or spreading, branches often fascicled, closely appressed to widely spreading or reflexed; spikelets 3.5–7 mm. long, averaging 4.5 mm., florets usually 1, occasionally 2; glumes sub-acute to obtuse, usually shorter than last floret, first glume 2–5 mm. long, average 3 mm., second glume 2.5–6 mm. long, average 3.5 mm.; lemmas not pubescent above, apex acute to obtuse, first lemma 3–7 mm. long, averaging 4.5 mm.; palea as long as lemma; rudiment long, obtuse-oblong, 0.5–4 mm. long, averaging 2 mm., stipe shorter than rudiment.

Type. "California." The type, if it now exists at all, is presumably in the Academy of Science at Leningrad.

Range. Lower California to north central California, principally in the coast ranges, rare in the central Sierra Nevada below 4000 feet; chiefly on dry, rocky hillsides or open dry woods.

Representative specimens. CALIFORNIA. Kern County: Kern Canyon, *Heller 7652* (UC, G, M, NY, S). Los Angeles County: Santa Catalina Island, *Fosberg 84430* (UC, NY). Monterey County: Tassajara Hot Springs, *Ferris 8328* (UC, G, CA, S); Pacific Grove, *Heller 6737* (G, M, NY, S). Santa Barbara County: Santa Barbara, *Elmer 3787* (UC, G, M, NY, S). Santa Clara County: near Los Gatos, *Boyle 1064*. San Diego County: Moro Hills, *Abrams* (G, M, NY, S).

The variety *refracta* is reputedly distinguished from the species by the spreading branches and dense pubescence. The variety *flexuosa* is likewise supposedly unique in the possession of widely spreading or reflexed branches. Actually, pubescence and position of the branches varies indiscriminately throughout this group with no geographic segregation of either of these two characters. The variety *minor* is believed simply to be applicable to depauperate specimens.

12. *MELICA FRUTESCENS* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 45. 1885.

Culms up to 2 m. long, stout, often slightly woody at base, branches often arising near culm base; blades 2–4 mm. wide; panicle 12–40 cm. long, averaging 20 cm., narrow and dense, occasionally interrupted below, pale and shining or rarely purpletinged; spikelets 12–18 mm. long, averaging 14 mm., florets 3 to 6, usually 4; glumes papery, first glume 7–12 mm. long, averaging 9 mm., second glume 9–15 mm. long, averaging 11 mm.; lemmas usually obtuse, upper third papery-scarious; first lemma 8–11 mm. long, averaging 9.5 mm.; palea usually about half the length of lemma; anthers 2 mm. long; caryopses 2–3 mm. long; rudiment 4.5–6.5 mm. long, consisting of a fairly large sterile lemma enclosing a globose rudiment proper.

Type. Southern California, *Parry and Lemmon 401*, 1876. The type is assumed to be in the United States National Herbarium.

Range. From Inyo County in southern California south to Lower California and south-central Arizona; chiefly on dry hills, flats and foothill ranges of the desert country.

Representative specimens. CALIFORNIA. Victorville, 1903, *Jones* (G, W). San Diego County: Bernardo, *Abrams 3361* (G, M, NY, CA, S); Colorado Desert, *Munz and Hitchcock 12050* (UC, M). LOWER CALIFORNIA. Socorro Canyon, *Wiggins 5219* (US, S).

The seeds of *M. frutescens* possess, so far as is known, greater viability than those of any other species in the genus. Caryopses from a five-year-old herbarium specimen exhibited seventy-five per cent germination. The marked viability of seeds, rapid vegetative growth, production of branches near the culm base, self-fertility and its marked resistance to drought are features of considerable interest in relation to the development of better forage on our western range lands.

13. *MELICA MONTEZUMAE* Piper, Proc. Biol. Soc. Wash. 18: 144. 1905. *M. alba* Hitchcock, Contr. U. S. Nat. Herb. 17: 367. 1913.

Culms up to 1 m. long, loosely tufted; blades 1–3 mm. wide, apices indurate, ligules 5–10 mm. long; panicle 5–25 cm. long, averaging 16 cm., open, branches ascending to reflexed, distant; spikelets 6–8 mm. long, pale, shining, fertile floret 1, articulation below the glumes; glumes usually as long as floret, first glume 7–8 mm. long, very broad, somewhat enfolding spikelet, second glume 7–8 mm. long, considerably narrower; lemma 7–8 mm. long, oblong-truncate, very thick, greenish and tuberculate-roughened except for marked scarious apex and bearing a group of flat, twisted, glass-like hairs on back, nerves prominent, many; anthers 2–3 mm. long, rudiment oblong-truncate, 2–3 mm. long.

Type. Santa Eulalia Mts., Chihuahua, Mexico, April 6, 1885, Pringle 430 (US).

Range. Mountains of northern Mexico and southwestern Texas; apparently in shaded, protected sites.

Representative specimens. TEXAS. Brewster County: Chisos Mts., Cory 18657 (G). Pecos County: Sheffield, Jones 26362 (M, S). MEXICO. Chihuahua: Santa Eulalia Mts., Pringle 430 (G, M, US, type; WS). Coahuila: San Lorenzo Canyon, Palmer 551 (UC, G, NY).

This species has not previously been reported from the United States. It is probably most closely related to *M. nitens*. A form of the latter species in southwest Texas exists which occasionally has but one floret and a similar rudiment; *M. montezumae* may have arisen from that source.

14. *MELICA MUTICA* Walt. Fl. Carol. 78. 1788. *M. altissima* Walt. Fl. Carol. 78. 1788 (not *M. altissima* L.). *M. glabra* Michx. Fl. Bor. Am. 1: 62. 1803. *M. rariflora* Schreb. Besch. Gräs. 2: 157. 1810. *M. diffusa* Pursh, Fl. Am. Sept. 1: 77. 1814. *M. racemosa* Muhl. Descr. Gram. 88. 1817. *M. speciosa* Muhl. Descr. Gram. 87. 1817. *M. Muhlenbergiana* Schultes, Mant. 2: 294. 1824. *M. mutica* var. *glabra* Gray, Man. ed. 5, 626, 1867. *M. mutica* var. *diffusa* Gray, Man. ed. 5, 626. 1867. *M. mutica* f. *diffusa* Fernald, Rhodora, 41: 501. 1939.

Culms up to 100 cm. long, arising from a rhizome; blades 2–6 mm. wide; panicle 4–16 cm. long, averaging 13 cm., simple, rarely compound, open, branches ascending or spreading; spikelets 7–11 mm. long, averaging 9 mm., nodding to pendulous, florets spreading, spikelets V-shaped, flat-topped, apices of first two florets very nearly same height, rachilla somewhat flattened, fertile florets 2, rarely more, articulation below glumes; glumes subequal, margins and apices very scarious, first glume 6–9 mm. long, averaging 7 mm., second glume 6–9 mm. long, averaging 8 mm., as long or nearly as long as spikelet; lemmas very firm, ridged on

back, first lemma 6–11 mm. long, averaging 8 mm., nerves prominent; anthers 3 mm. long; caryopses 2–3 mm. long; rudiment very blunt, obconic, 2–4 mm. long, inner sterile lemmas almost invariably extruded, rudiment usually bent at an angle toward rachilla.

Type. "South Carolina." The existence of the type is very uncertain. The following specimen may be considered as representative of this species: *E. B. Harger* 7784, dry woods on Walden Ridge, Pikeville, Bledsoe County, Tennessee (G).

Range. Maryland to Florida and west to eastern Texas and Oklahoma; in moist, rich or dry, open woods and thickets.

Representative specimens. GEORGIA. De Kalb County: Stone Mt., 1895, *Small* (NY, M, G, CA). NORTH CAROLINA. Buncombe County: Biltmore Herbarium 645b (UC, G, M, NY, W, US). OKLAHOMA. McCurtain County: Shawneetown, *Houghton* 3882 (G, M, NY). SOUTH CAROLINA. Horry County: Myrtle Beach, *Griscom* 511 (UC, G, M, W, BC, CA, S).

15. *MELICA NITENS* (Scribn.) Hitch. Man. Grasses U. S. 201. 1935. *M. scabra* Nutt. Trans. Amer. Phil. Soc. 5: 148. 1837. *M. nitens* Nutt. in herb. *M. diffusa* var. *nitens* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 44. 1885.

Culms up to 120 cm. long, arising from a rhizome; blades lax, 3–15 mm. wide, averaging 7 mm., panicle 6–26 cm. long, averaging 20 cm., wide, compound, branches widely spreading or ascending; spikelets 8–15 mm. long, averaging 11 mm., florets 1 to 4, usually 3, second floret usually exceeding first by 2 mm., nodding to pendulous, articulation below glumes; glumes subacute, first glume very broad, 5–7 mm. long, second glume narrower, 7–9 mm. long, and usually 1 mm. shorter than spikelet; lemmas acute to emarginate, first lemma 8–11 mm. long, averaging 9 mm., very firm but less indurate and ridged than in *M. mutica*; anthers 3 mm. long; rudiment oblong club-shaped, never bent at angle to rachilla, inner sterile lemmas not extruding, 1–4 mm. long, usually 2.5 mm.

Type. Designation of the type is very difficult owing to the confusion of the synonymy. It is presumably the collection first cited by Scribner (9) under var. *nitens* of *M. diffusa*: *J. Reverchon* 3464a, Texas.

Range. Pennsylvania and Virginia west to Kansas, Nebraska and western Texas. (Specimens have been reported from New Mexico and Arizona.) Habitat variable, rich soil in open woods to rocky woods, bluffs and flats.

Representative specimens. ILLINOIS. Peoria County: Peoria, 1912, *Churchill* (G, M, NY). IOWA. Storey County: Ames, *Ball* 33 (NY, M, US). KANSAS. Riley County: Woods, *Norton* 935 (G, M, NY, W, US). MISSOURI. Meramec, 1879, *Eggert* (NY, M, W, BC). OKLAHOMA. Comanche County: Fort Sill, *Clemens* 11487 (M, NY, W).

16. *MELICA STRICTA* Bolander, Proc. Calif. Acad. Sci. 3: 4-5. 1863.

Culms up to 85 cm., densely tufted, anthocyanous near the base (except in var. *albicaulis*), lower portion thickened but not bulbous; blades 2-5 mm. wide; panicle 3-30 cm. long, averaging 14 cm., narrow, simple, branches appressed; spikelets 6-23 mm. long, averaging 16 mm., broadly V-shaped when mature, articulation below the glumes, florets 2 to 5; glumes acute to emarginate, first glume 6-16 mm. long, averaging 13 mm., second glume 6-18 mm. long, averaging 14 mm., as long or nearly as long as the spikelet; lemmas obtuse to acute, first lemma 8-16 mm. long, averaging 12 mm., palea one-half to two-thirds as long as lemma; caryopses 4-5 mm. long; anthers 1-2 mm. long (as long as 3 mm. in var. *albicaulis*); rudiment narrow, tapering above, 2-7 mm. long, averaging 5 mm.

Type. Silver City, Nevada, *G. W. Dunn* (G).

Range. Southern Oregon to southern California eastward to Utah; rocky slopes or open woods; extends to alpine areas.

Representative specimens. CALIFORNIA. Humboldt County: Salmon Summit, *Tracy 14377* (UC, G, S). Nevada County: Castle Peak, *Heller 7078* (UC, G, M, NY, W, O, S). Tulare County: Alta Peak, *Long 245a* (UC, NY, BC, W, WS, CA). OREGON. Harney County: Steens Mts., *Cusick 1972* (UC, M, US, BC, O, WS).

16a. *MELICA STRICTA* var. *albicaulis* var. nov. Vaginae culmorum inferiorum stramineae pallidae, palea longum dodrans lemmae, antherae 2-3 mm. longae.

The variety *albicaulis* differs from the species in the following characters: (1) sheaths of lower portion of culms pale straw color, (2) palea three-fourths the length of lemma, (3) anthers 2-3 mm. long, (4) glumes more broad, more hyaline and less acute than in the species.

Type. Coldwater and Lytle creeks, San Antonio Mts., California, dry ground under pines, elevation 7000 feet, July 3, 1917, *I. M. Johnston 1516* (UC).

Range. Mountains of southern California.

Representative specimens. CALIFORNIA. Ventura County: Frazier Mts., 1934, *Epling* (UC, M). Los Angeles County: San Gabriel Mts., *Abrams 614* (G, NY, S). San Bernardino County: San Antonio Mts., *Johnston 1516* (UC, type; US, W, S); San Bernardino Mts., *Parish 3699* (UC, G, CA).

This variety is based more upon its marked geographic segregation than upon strong morphological divergence from the species.

17. *MELICA PORTERI* Scribn. Proc. Acad. Nat. Sci. Phila. 37: 44. 1885. *M. mutica* var. *parviflora* Porter, Porter and Coulter,

Syn. Fl. Colo. 149. 1874. *M. parviflora* Scribn. Mem. Torrey Bot. Club 5: 50. 1894.

Culms up to 100 cm. tall, loosely tufted, arising from a rhizome; blades 2–6 mm. wide; ligule 3–7 mm. long; panicle 13–25 cm. long, averaging 21 cm., narrow to open (in var. *laxa*); spikelets 8–16 mm. long, averaging 12 mm., often secund on the branch; glumes subequal, very short, usually one-half the length of spikelet, occasionally two-thirds; first glume 4–6 mm. long, second glume 5–8 mm. long, averaging 6.5 mm., lemmas tapering to rounded apex, first lemma 6–10 mm. long, averaging 7.5 mm.; anthers 2 mm. long; caryopses 2–3 mm. long; rudiment narrow, tapering upward, 2–5 mm. long.

Type. Glen Eyrie, near Colorado City, Colorado, July, 1872, T. C. Porter. The type is assumed to be in the United States National Herbarium.

Range. Northern Colorado south to the Sierra Madre Range in Mexico, westward to Arizona and eastward to central Texas; rocky slopes and open woods.

Representative specimens. COLORADO. Southern Colorado, Baker 186 (G, M, NY, US, W). El Paso County: 6000 ft., Shear 726 (G, NY, US). San Miguel County: stream bank, Maguire 12694 (G, M, WS, W). NEW MEXICO. Socorro County: Mogollon Mts., Metcalf 283 (UC, G, M, NY, W).

This species was grown easily from seed without stratification despite the fact that this is a species characteristic of high elevations.

17a. *MELICA PORTERI* var. *laxa* var. nov. Rami late extensive ascensi, spiculae purpureae tinctae, glumae pro portione specie breviores.

Variety *laxa* differs from the species in the following morphological features: (1) branches widely spreading or ascending-spreading, (2) spikelets purple-tinged, (3) glumes proportionately longer, (4) rudiment less acute and shorter in length.

Type. White Mts., New Mexico, 7000 feet, August 13, 1897, E. O. Wooton 680 (NY).

Range. Mountains of southern New Mexico and Arizona, and the Chisos Mountains of western Texas.

Representative specimens. ARIZONA. Chiricahua Mts., Blumer 1494 (G, M, W). Rincon Mts., Blumer 3444 (UC, M, S). Santa Rita Mts., Pringle 15985 (G, M, NY). NEW MEXICO. Lincoln County: White Mts., Wooton 680 (NY, type; M); Wooton 35533 (UC, G, WS, S).

NAMES EXCLUDED

Melica anomala Scribn. in Beal, Grasses N. Am. 2: 311. 1896
= *MUHLENBERGIA LONGILIGULA* Hitch.

Melica argentea (Howell) Beal, Bull. Torrey Bot. Club 17: 153.
1890 = *POA PRINGLEI* Scribn.

- Melica Hallii* Vasey, Bot. Gaz. 6: 296. 1881 = *FESTUCA SCABRELLA* Torr.
Melica macrantha Beal, Bull. Torrey Bot. Club 17: 153. 1890 = *POA MACRANTHA* Vasey.
Melica multinervosa Vasey, Bot. Gaz. 16: 235. 1891 = *VASEYCHLOA MULTINERVOSA* (Vasey) Hitch.
Melica nana Beal, Grasses N. Am. 2: 504. 1896. Based on *MELICA ARGENTEA* (Howell) Beal; see above.
Melica purpurascens Hitch. Contr. U. S. Nat. Herb. 12: 156. 1908 = *SCHIZACHNE PURPURASCENS* (Torr.) Swallen.
Melica striata Hitch. Rhodora 8: 211. 1906 = *SCHIZACHNE PURPURASCENS* (Torr.) Swallen.

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M. FRENCH GILMAN

Marshall French Gilman, grandson of the first white couple to settle in the San Geronio Pass of southern California, died July 18, 1944, after some months of illness. Born November 12, 1871, at Banning, California, French Gilman had a long career of service: as a teacher at Upland, California; postmaster and then horticultural inspector and deputy state quarantine officer at Banning; assistant postmaster and secretary of the Palm Valley Water Company at Palm Springs; teacher and officer in schools in the United States Indian Service at Fort Lewis, Colorado, Shiprock, New Mexico, Sacaton, Arizona, and Fort Bidwell, California; clerk of the high school board at Banning; councilman, member of forestry board of Riverside County, and mayor of Banning.

For many years a rancher and fruit-grower, he was always interested in scientific method and cooperated in many ways with the United States Department of Agriculture, particularly with Dr. W. T. Swingle, supervising experimental cotton plantings near Palm Springs, establishing an experimental station of possible food and medicine plants on the Papago Indian Reservation in Arizona, and carrying out on a small plot at Banning experiments on propagation and cultivation of a Chinese species of *Ephedra*, a *Solanum* from Siam, and on budding and grafting cultivated fruits on native plum roots. He was joint author of a paper on *Ammobroma sonora* Torr. with Frank A. Thackery of the Department of Agriculture (A rare parasitic food plant of the southwest. Ann. Rept. Smithsonian Inst. 1930: 409-416. 9 pl. 1931).

In 1899 he married Sarah Morris, a teacher at the Morongo Indian Reservation. Blind in her later years, Mrs. Gilman was unable to accompany her husband to Death Valley when it became financially necessary for him to take employment there with the National Park Service. I remember well on July 8, 1937, when a party of us climbed Telescope Peak in the Panamint Mountains, how Mr. Gilman sat down, pulled out writing materials, and wrote a letter home, saying that he always wrote Mrs. Gilman from the



FIG. 1. French Gilman.

top. The modest Gilman home at Banning was always open to friends. Here was real hospitality and rare charm, and a delight on the part of the owners to tell about their treasures, particularly their large collection of Indian baskets. Mrs. Gilman died in 1941.

Mr. Gilman was an authority on southwestern birds, and on field trips for plants was always observing and identifying birds. The Sahuaro Screech Owl (*Otus asio gilmani*) bears his name. Between the years 1902 and 1937 he published twenty-five articles or notes in Condor and in 1930 he had a paper on "Cacti as nesting sites" in the Journal of the Cactus and Succulent Society of America.

I best knew French Gilman through his interest in plants, collections of which he had made in his various regions of residence and which he had submitted to various herbaria for study. His name will be best and longest known, however, in connection with the flora of Death Valley, to which he began to devote especial study in assisting the late Dr. F. V. Coville in his survey of plants of that area. Then, as acting custodian of Death Valley National Monument for some months in 1933 and 1934, and later in charge of a nursery and small botanical garden there, he devoted several of his last years to the native plants of that region, remaining there even through the hot summers to maintain his nursery. His plantings were visited by thousands of visitors and his evening talks on the plants of Death Valley made him known to many others.

It is a tribute to his energy and industry that he was able during his several years in Death Valley to add so many species to the list known for the region. A few examples that happen to occur to me, some of which were even new to California are: *Betula fontinalis* Sarg., *Stipa arida* Jones, *Oenothera scapoidea* Nutt. var. *seorsa* (Nels.) Munz, *Angelica lineariloba* Gray, *Mimulus montioides* Gray, *Laphamia intricata* Brandg., *L. megacephala* Wats., *Senecio spartioides* T. and G., and *S. uintahensis* (Nels.) Greenman. Then he either collected, or was in the party which collected, many plants new to science; of these the following list is very incomplete: *Eriogonum Gilmanii* Stokes, *E. intrafractum* Cov. and Morton, *E. mensicola* Stokes, *E. panamintense* Morton, *Petalonyx Gilmanii* Munz, *Oenothera dentata* Cav. var. *Gilmanii* Munz, *Cymopterus Gilmanii* Morton, *Gilia Gilmanii* Jepson (a later synonym of *Gilia Ripleyi* Barneby), *Phacelia mustelina* Cov., *Salvia carnosa* Dougl. subsp. *Gilmanii* Epling, *Maurandya petrophila* Cov. and Morton, *Mimulus rupicola* Cov., *Cordylanthus eremicus* (Cov. and Morton) Munz. Dr. Coville (Jour. Wash. Acad. Sci. 26: 209-213. 1936) proposed in his honor the genus *Gilmania* for that rare plant formerly known as *Phyllogonum luteolum* Cov.

Those who knew French Gilman loved him. His kindness, honesty, sincerity, enthusiasm, ability to face adversity—all these

qualities naturally endeared him to many. I count it as one of my great privileges to have had as a friend this man—self-taught and wise. It is good that his name shall live long in the botanical annals of California.—PHILIP A. MUNZ, Bailey, Hortorium, Cornell University, Ithaca, New York.

AN ABNORMAL PEPPERGRASS

C. L. HITCHCOCK

During the course of a taxonomic study of the *Lepidia* of the Western Hemisphere one specimen has been seen which is so unusual that it is felt a brief description of it will be of interest to others. This plant was collected at Charcas, San Luis Potosi, Mexico, in 1934 (*Alfred F. Whiting 914EB*, United States Herbarium number 1688427). It is a teratological specimen, and so greatly modified that it is difficult to make a determination to species, but it is believed that it is *L. Schaffneri* Thellung. The branches of the plant end in one or more racemes at the base of which there remain numerous pedicels supporting all that is left of the ripened silicles—the placentae and repla. Apparently these fruits produced normal seeds.

The flowers of the upper half of each raceme are progressively more and more modified. A practically normal fruit and a normal flower are to be seen in figure one. Two stamens, four sepals, four petals, and four glands are common to all ordinary flowers of the species. Figure two represents one of the little-altered flowers of the specimen. It will be noted that there are two stamens which apparently are fertile, four sepals, four short linear petals (one of which has been removed, the more easily to show the bud beneath it), and rudimentary branches that had started to develop where the "glands" should be. The silicle is enlarged, pubescent, and considerably modified internally, with basal branches developing as shown in figure three. That drawing (plate 2, fig. 3) illustrates an opened fruit bearing a small partially developed branch in the axil of each valve. The two ovules are recognizable as such, although the funiculi are freed from the placentae below their normal point of attachment in the silicle. The replum is lacking entirely.

Figure four shows a flower that is more greatly modified. In place of ovules there are leaf-like structures where ovules might normally be. The branches that originate in the axils of the valves are larger and fastigate in appearance. The flower drawn in figure five is essentially similar to that of figure four, but all trace of the ovules has disappeared. Figure six represents a case in which a main branch has grown from the center of the fruit, one "axillary bud," only, developing. Figure seven shows a flower

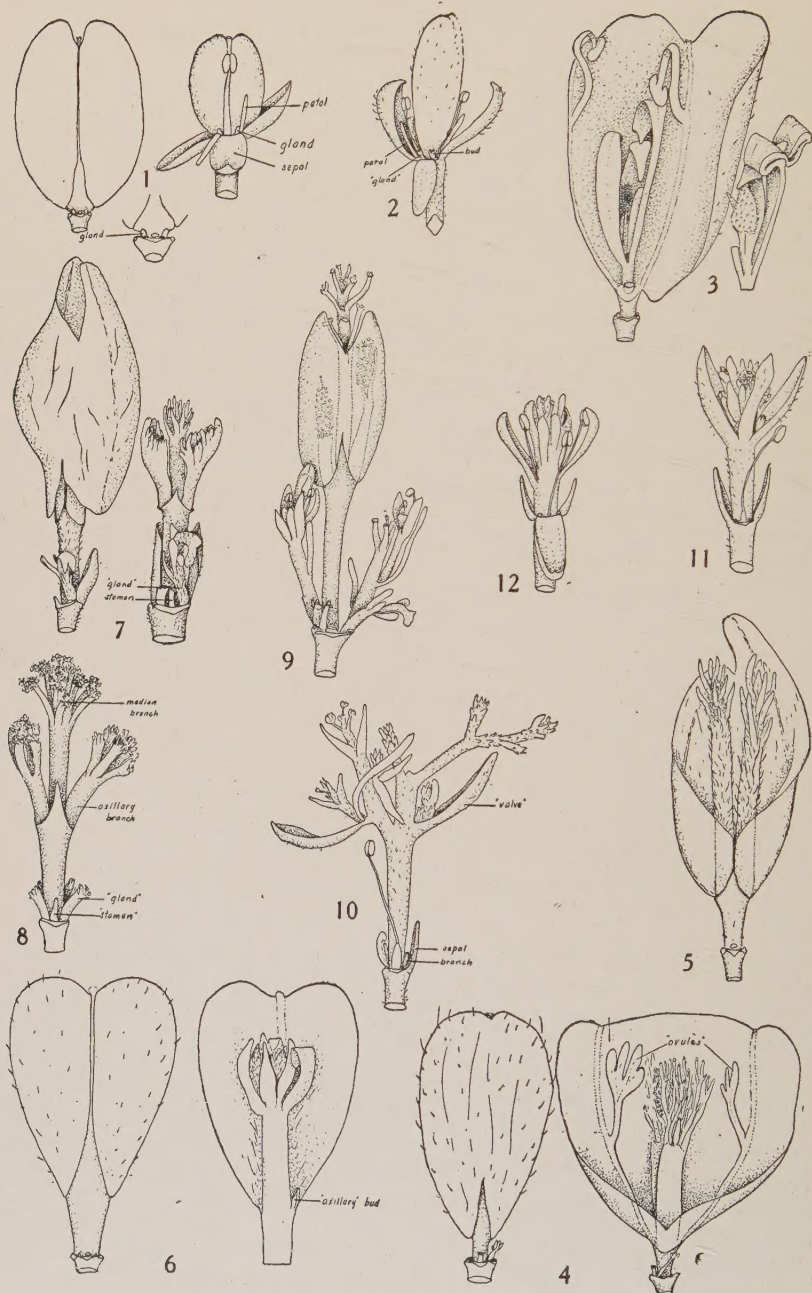


PLATE 2. A TERATOLOGICAL SPECIMEN OF *LEPIDIUM*.

in which two branches have developed from the region of the "glands." In the ovary itself, three branches have developed, one from the "axil" of each valve, the third median to these two. Figures eight, nine, and ten are illustrations of flowers that are essentially similar to the previous one; in figure nine the branches from the "glands" are more fully developed. Stamens and ovaries have developed in the axils of a few of the bracts on these branches. The flower of figure ten is so modified that one can but compare, by virtue of their position, the subtending basal bracts of the upper branches to the valves of a silicle. Figures eleven and twelve represent a couple of flowers that have produced central branches in the position normal for the fruit. Sepals, petals, and stamens are not greatly altered in appearance.

Although it is realized that general deductions concerning morphological structures cannot safely be drawn from teratological material, these points are of interest at least: 1. Floral branches from below the ovary apparently have arisen in each case from the position considered "normal" for the glands of the flower. 2. In most cases a branch has developed from the "axil" of each valve of the silicle. 3. Judged from the number of branches that develop in the ovary, there is no indication that there are four carpels in the flower.

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REVIEW

Foundations of Plant Geography. By STANLEY A. CAIN. Pp. xiv + 556 and 63 figures. Harper & Brothers, 1944. \$5.00.

This is undoubtedly the most comprehensive and modern book on plant geography written from the historical point of view. Its comprehensiveness is indicated both by its length and the number of titles, 720, in the section on "Literature Cited." Its modernity is evident from the fact that nearly two-thirds of these titles represent works written since 1930. For these reasons alone it is a "must have" for the library of every serious botanist or botanical institution. No where else can one find such a wealth of recent material on this subject carefully and impartially reviewed.

To readers of Madroño Dr. Cain's book is of particular significance for two reasons. In the first place, its basic framework is taken from the principles published by our editor, Dr. Mason, in this journal (vol. 3, pp. 181-190). Secondly, both the history of the flora of the western United States and the work of western botanists receive particular emphasis. The figures include no less than eight outline maps of California and the adjacent states, which illustrate the distribution of such familiar and interesting groups as *Sequoia*, *Libocedrus*, *Pinus Jeffreyi*, *Pentstemon* spp., and *Crepis*. An outline map of the Monterey Peninsula, illustrating

the distribution of its interesting conifers, is the only map of a local area which is included.

Although clearly written and well organized, Dr. Cain's book will undoubtedly be of more value to advanced students and mature botanists than to beginners or amateurs. It is a reference book rather than a textbook or popular work. As such, its value is enhanced both by its comprehensiveness and the balanced impartial viewpoint of its author. All material pertinent to the subject, whether obtained from paleontology, population studies, cytogenetics or the more classical approach of the mapping of modern species distributions, is given ample consideration. Such controversial viewpoints as those held by Clements, Willis, and Wegener are treated as objectively as possible, with due consideration given to the arguments on both sides. The author, however, is clearly more interested in patterns of distribution of species and genera in relation to evolution than in plant associations and climate; in other words, the book treats with historical rather than ecological plant geography. The five principal divisions of the book are, in fact, I, Introduction (28 pp.); II, Paleoecology (118 pp.); III, Areography (173 pp.), including such topics as Dispersal and Migration, Center of Area, Center of Origin, and Endemism; IV, Evolution and Plant Geography (77 pp.); and V, Significance of Polyploidy in Plant Geography (30 pp.).

In such an extensive work some minor errors are inevitable. For instance, in the phylogenetic tree of the California closed cone pines on page 113, *Pinus attenuata* is interpreted as a Pleistocene derivative of *P. linguiformis*, whereas on page 83 a reproduction of Axelrod's list of species from the older Mount Eden Pliocene beds includes a counterpart of *P. attenuata*, listed under the synonym, *P. tuberculata*. Also, on page 217 a table showing the endemism in the Galapagos Islands includes figures on the "Maximum Altitude in M.," which range from 210 up to 5000, and agree with published maps only when read as feet, not meters. The discussion of the cytogenetic evidence is accurate and well balanced, although somewhat redundant, as evidenced by the quotation of a paragraph from one of this reviewer's papers, which he does not consider of particular significance, in two different places (pp. 239 and 469). The format, typography, and illustrations are in general clear and attractive, although the number of typographical errors is not inconsiderable.

Dr. Cain has done a great service to all students of plant geography and evolution. His work will continue to be of primary significance for many years to come.—G. LEDYARD STEBBINS, JR., Division of Genetics, University of California, Berkeley.